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Edges effects on seed predation by rodents in deciduous forests of northern Switzerland

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Abstract

Seed predation by rodents affects plant population dynamics and it may respond to changes in vegetation structure at forest edges. This study investigates the magnitude and direction of a potential edge effect in temperate deciduous forests, and it seeks possible explanations based on predator abundance and vegetation structure. The study was conducted at twelve forest edges in northern Switzerland; in six sites all shrubs at the forest edge were removed, whereas the other sites maintained a structurally rich shrub layer. In each site three transects were laid out from the edge towards the forest interior. In six plots along these transects (at 1, 3, 6, 12, 25, 50 m) we studied seed removal from experimental dishes, rodent abundance in live-traps and four characteristics of the vegetation structure. For both woody seed species (*Prunus avium*, *Viburnum lantana*) predation was significantly higher near the forest edge in the structurally rich sites; in the other sites no such gradient was found. Selectively accessible dishes revealed that rodents were the main predators, whereas predation by insects or molluscs was not observed. Abundance of rodents (*Apodemus flavicollis*, *A. sylvaticus*, *Clethrionomys glareolus*) was highest under dense shrubs close to the forest edge. In the structurally rich sites there was a clear gradient of decreasing shrub cover from the edge towards the forest interior; a weaker gradient was observed in the structurally poor sites. We conclude that high shrub cover near the forest edge is the main determinant for edge effects in seed predation, and edges without a shrub belt show no such effect.

Introduction

Fragmentation, disturbance and destruction of forests are among the most pressing ecological problems in many parts of the world with negative consequences for biodiversity (Saunders et al. 1991; Collinge 1996; Turner 1996; Zuidema et al. 1996). Fragmentation increases the fraction of forest which is close to open land and where edge effects may occur. The distance over which edge effects can be observed depends on the specific process, although most effects are found within 50 m from the forest edge (Matlack 1993; Murcia 1995; McCollin 1998). It is useful to differentiate between abiotic and biotic components of any "edge effect". Abiotic components are patterns in microclimate and soil conditions near the forest edge (Chen et al. 1993, 1995). Direct biotic edge effects describe changes in species abundance, for example of tree species due to reduced rejuvenation and increased mortality near the forest edge (Williams-Linera 1990; Chen et al. 1992). Indirect biotic edge effects, on the other hand, are caused by other organisms which lead, for example, to increased nest predation, higher brood parasitism or more intense seed predation close to the edge (Brittingham and Temple 1983; Gibbs 1991; Paton 1994; Jules and Rathcke 1999).

Post-dispersal seed predation is an important candidate for an indirect biotic edge effect, because this process may affect plant recruitment and vegetation dynamics (De Steven 1991; Heske et al. 1993; Reader 1993; Hoffmann et al. 1995; Wijdeven and Kuzee

2000). Predation reduces the chances for reproduction especially in species which have no vegetative reproduction, develop no persistent seed bank, have no mast seeding, and are not limited by the availability of safe sites (Andersen 1989; Hulme 1998). Little is known about seed predation with respect to forest edges, and most published studies were performed in tropical forest fragments (Burkey 1993; Osunkoya 1994; Notman et al. 1996; Holl and Lulow 1997; Tabarelli and Mantovani 1997; Wong et al. 1998; Restrepo and Vargas 1999), while only two studies investigated temperate forest edges (Sork 1983; Jules and Rathcke 1999). This survey of the literature excludes studies which infer seed predation indirectly by recording changes in seedling densities with increasing distance to the edge (e.g. Benitez-Malvido (1998)).

The results of the nine studies on seed predation at forest edges are contradicting. Tabarelli and Mantovani (1997); Jules and Rathcke (1999) found higher seed losses near the edge compared with forest interior, whereas Sork (1983); Burkey (1993); Osunkoya (1994); Restrepo and Vargas (1999) reported lower predation near the edge, and no significant differences were detected by Notman et al. (1996); Holl and Lulow (1997); Wong et al. (1998). However, extrapolation of edge effects from tropical studies to the temperate zone might be spurious, because of fundamental differences between temperate and tropical ecosystems as shown by Söderström (1999) for edge effects in nest predation. The results suggest that even within one biome, the effect of forest edges on seed predation may vary depending on forest community, management of the forest edge, adjacent habitat, aspect of the edge and seasonal differences. Moreover, the seed species offered and the predator guilds (rodents, birds, insects, molluscs) differ between sites and regions. Thus, new experiments are needed which unravel the site-specific mechanisms of edge effects in seed predation, i.e. identify the responsible animals and analyse the vegetation structure which is related to their habitat preferences, especially in temperate forest ecosystems.

As suggested by McCollin (1998) for bird abundance, we suppose that many "edge effects" are not simply a result of the forest edge *per se*, i.e. direct and largely abiotic effects of the border between forest and open land, but that they are caused by associated changes in vegetation structure near the edge. Therefore, a precise description of the edge structure is desirable for studies on edge effects in seed predation. Even in relatively small regions, such as central Europe, forest edges have no uniform structure: some are rather open due to recent disturbance or clear-cutting, in some the trees develop dense foliage even near the ground, whereas in others there is a clear zonation of tall herbs, shrubs and light-demanding trees (Ellenberg 1988; Richert 1996). In addition, one has to differentiate between external edges (bordering agricultural land), internal edges (forest gaps or tracks) and those between different forest stands (age classes or community types). The novel approach of the present study is to investigate seed predation in a homogenous sample of forest edges with standardized topography, similar aspect, forest types and adjacent vegetation. For half of these sites we experimentally changed shrub cover at the edge, because vegetation cover close to the ground explains a high percentage of variation in post-dispersal seed predation in temperate ecosystems (cf. Gill and Marks (1991); Kollmann (1995); Hulme (1997)). Thus, our approach investigates the notion of Ranney et al. (1981); Matlack (1993); Murcia (1995) that edge effects can be modulated by the specific structure of the forest edge.

Ground vegetation and seed predation were investigated with highest resolution close to the forest edge, because (1) considerable variation in vegetation structure was expected for this part of the edge gradient (Ellenberg 1988), (2) rodent abundance responds to small-scale changes in habitat structure (e.g. Schreiner et al. (2000)), and (3) this part of the gradient has been neglected in some of the earlier studies (e.g. Burkey (1993); Jules and Rathcke (1999)). Along transects, key variables of the forest vegetation were recorded which might be related to the habitat preferences of seed predators. The identity of the predators was investigated with selectively accessible dishes and live-traps. For the predation experiment seeds of two fleshy-fruited woody species were chosen, which are common along temperate forest edges (Kollmann 1997; Kollmann and Schneider 1999), which produce a high (bird-mediated) seed rain along the edges (Hoppes 1988), and which might be limited in reproduction by seed predation as show for *Trillium ovatum* in western North American conifer forest (Jules and Rathcke 1999).

More specifically, we focus on the following questions which can be answered by the data of our study:

- Are the rates of seed predation affected by distance to the edge of a deciduous temperate forest?

- Is a potential edge effect caused by the forest edge *per se* or by associated changes in vegetation structure?
- Which characteristics of the edge vegetation are correlated with high predation rates?
- Which animals are responsible for seed predation and what are their habitat preferences?

Study sites and methods

Study sites

The study took place at forest edges in the surroundings of the village Hemmental in northern Switzerland (1078 ha; 47°44–45′ N, 8°33–37′ E). This area is suitable because the landscape mosaic has been stable for a long time and the percentage of forest is relatively high (68%, Huber and Egli (1998)). Moreover, the vegetation along the forest edges is structurally diverse and species-rich (Kollmann and Schneider 1999), and has been maintained by intermittent cutting of the shrub belt every 5–10 year. The bedrock is limestone ("malm"; Hofmann and Hübscher (1977)). Annual precipitation averages 800–900 mm, average annual temperature is 8°C (Waldvogel and Graf 1981).

After a general survey of all forest edges in the study area, we selected twelve deciduous forest stands which were at least 500 m deep and for the first 100 m not affected by tracks, treefall gaps or clear cuts. The forests were mesic to moderately dry beech communities (Galio-Fagetum and Carici-Fagetum; Ellenberg (1988)), bordered by nutrient-poor grasslands (Arrhenatheretum and Mesobrometum). All edge sites were SE-W facing, showed no signs of recent disturbance except cutting of the shrub layer, and were separated by a distance of 150–1000 m to achieve independence of the replicated sites. We selected six forest edges with an intact shrub layer ("structurally rich edges") and six edges where the shrubs had been recently cut, mostly in the preceding winter ("structurally poor edges"). The two edge types were differentiated based on shrub cover (0.5–3.0 m height) at 0–1 m distance from the edge: structurally rich edges had a shrub cover of 70–90%, structurally poor sites 30–60%. All forest edges followed a straight line. The forest stands were situated at 580–835 m a.s.l. (mean 746 m), had a slope inclination of 11–52% (mean 34°), and most were at least 300 years old (Huber and Egli 1998). The two edge types were intermixed in the study area, and they did not differ significantly in forest community, age, altitude, inclination and aspect.

Design of the study

In each site three 50 m long transects were laid out from the edge towards forest interior, with a distance of 10 m between transects. We defined forest edge as the border between herbaceous vegetation of the adjacent grassland and shrub-dominated vegetation of the forest edge where herbs and grass had a markedly reduced cover. At 1, 3, 6, 12, 25 and 50 m from the edge permanent plots were established to investigate intensity of seed predation, population density of rodents and vegetation structure. Seed predation was assessed in late June and late July 1999, rodents were trapped shortly before and after the predation experiments (mid June, early August), and the vegetation survey took place between the two experiments (early July).

Seed dishes

Seed predation was studied using paired Petri dishes (9 cm diameter) with a distance of 0.5 m, on a line perpendicular to the transects. In these feeding stations the seed were protected against rainfall by a second Petri dish which was suspended 15 cm above; the dishes were fixed to the ground by a small wooden stick. One feeding station was accessible to all potential seed predators (rodents, birds, insects, molluscs); here the top dish was supported by three bamboo sticks. In the second dish, rodents and birds were excluded by a wire cloth (1.3 cm net size) which also supported the upper dish. All dishes (216 open, 216 closed) were established with at least 0.5 m distance to tree trunks or dead wood to avoid locally increased rodent abundance. The set-up was identical for all sites and similar to Abramsky (1983); Willson and Whelan (1990); Hulme (1996, 1997); Kollmann et al. (1998); for critical comments on the seed dish technique see Kelrick et al. (1986).

We used seed of two fleshy-fruited European species which are common in the study area: the tree *Prunus avium* L. and the shrub *Viburnum lantana* L. Seeds of these species are large (*Prunus* 176 mg, *Viburnum* 36 mg) and highly attractive to rodents (Kollmann et al. 1998). Fruit material was collected from 3–5 individual plants per species in SW-Germany. The fleshy tissue of the fruit was mechanically

removed by sifting under cold running water. Seeds were dried at 30 °C, and thereafter stored at 5 °C; for further details see Kollmann et al. (1998).

For each experiment five seeds were offered per dish: seeds of *Prunus avium* in late June, *Viburnum lantana* in late July. Parasitised seeds were excluded because they are less attractive (Kollmann and Muir 1998). Gloves and special boots were worn for setting up the predation experiments to avoid interference with human odour, and labelling of the plots was minimal to avoid visual cues to the predators. Both experiments started during a period of fair, sunny weather when rodents are particularly active (Gurnell 1975). The dishes were checked after 1, 2, 4, 7, 11 and 16 days.

Survey of the vegetation structure

Four major characteristics of the vegetation were recorded in the 216 study plots: (1) percent cover of litter and soil in 1×1 m^2 plots; (2) percent cover of herbs and shrubs at 0–0.5 m (1×1 m^2), at 0.5–3 m and at 0–3 m height (both 3×3 m^2); (3) density of dead wood > 7.5 cm maximum diameter (5×5 m^2); and (4) density of trees with diameter at breast height > 7.5 cm (5×5 m^2).

Live-trapping of rodents

The populations of small mammals were sampled using 108 Sherman live-traps ($23 \times 9 \times 8$ cm^3). For three nights the traps were established at six randomly chosen edge sites; for the following three nights the traps were installed at the other six sites. The traps were baited with 10–20 sunflower seeds, and any catch was identified with Brohmer (1988) but not labelled before being released. In used traps the hay bedding was changed, because residual odour affects subsequent catches (Stoddart and Smith 1986; Gurnell and Little 1992; Tew et al. 1994). *Apodemus sylvaticus* and *A. flavicollis* were pooled for the statistical analyses due to uncertainities in species determination for young individuals (Corbet and Harris 1991).

Statistical analyses

Because the five seeds per dishes were not independent we used dishes as units of observation. For each dish there were observations from six days. To compare the rates of predation we calculated mean values of remaining seeds per dish over this time period. A dish was considered "empty" when over this period on average at least half of the seeds were gone; this definition allowed both for accidental losses of 1–2 seeds and for persistence of sterile seeds. To investigate only seed predation by rodents (birds), we used the dishes which were accessible for insects and molluscs to correct the data from the open dishes. However, with the exception of two control dishes with *Prunus avium* no seed losses were observed, and even here a correction was not justified because rodents were trapped in the same plots.

Because the study produced binary data ("dish empty" *vs* "dish full") rates of seed predation were analysed with logistic regressions (Sokal and Rohlf (1998), p. 767–778): $\log (p/(1-p)) = b_0 + b_1x_1 + b_2x_2 + \ldots + b_nx_n$, where p describes the probability that a dish is empty, $x_1, x_2 \ldots x_n$ are explanatory variables (e.g. *edge site, distance, site* × *distance*), b_0 the y axis intercept, and $b_1, b_2, \ldots b_n$ the slope of the regression model. *Edge site* had to be included as an explanatory variable because the three transects per site were not independent. We always tested two models with different sets of variables (*edge site, distance; edge site, distance, edge site* × *distance*). To find out which model was most suitable we applied Akaike's information criterion (AICc) which evaluates the models on the basis of the explained variance *vs* the number of parameters included (Burnham and Anderson 1998). It is defined as $AICc = -2\log L + 2K + 2K(K+1)/(n-K-1)$, where $-\log L$ describes the fit of the model, K the number of estimated parameters, and n the sample size. To compare the various models we calculated for each model the difference (ΔAICc) to the model with lowest AICc value. For ΔAICc 1–2 it is not possible to decide which model is more suitable, ΔAICc 3–7 characterizes less suitable models, whereas models with ΔAICc > 10 have to be rejected. In the results we present: (1) the likelihood ratio G^2 for each model (including the *P* value), (2) the Wald χ^2 test value (*P* value) for the explanatory variables, (3) the regression coefficient (incl. SE) of the variable *distance*, and (4) the AICc. The G^2 value describes whether or not the model is better than a reduced model with only the constant b_0 (Zar (1996), p. 469–470); the Wald χ^2 test investigates whether the model is improved by the respective variable.

In a second step we investigated which characteristics of the local vegetation structure explained most of the variation in seed predation. We exluded those variables which were significantly correlated with a

more suitable factor ($r_s > 0.6$ or $r_s < -0.6$; Lozàn (1992)). Spearman rank correlations were used, because the data were not normally distributed even after transformation. For example, in the case of the negative correlation between percent litter cover and percent open soil the latter was discarded because estimates were less reliable. Because the cover values of the three vegetation layers were positively correlated, total cover of the herb and shrub layer (0–3 m height; 3 × 3 m^2) was used instead of the individual results for herb (0–0.5 m) and shrub layer (0.5–3 m). The remaining variables, i.e. litter cover, cover of the herb and shrub layer, density of trees, density of dead wood, were included in a multiple logistic regression model. For those variables which showed a significant correlation with seed predation, we investigated whether or not they were affected by the distance to the forest edge (multiple linear regression; factors *edge site, distance* and *site* × *distance*).

In a third step the intensity of seed removal was compared with apparent rodent density (χ^2 test of independence). To correct for repeated trapping of the same individuals, only binary data were used, i.e. *no rodent* and *at least one rodent* trapped during three nights. We also calculated models for the relation between rodent activity (y) and vegetation structure (x).

No direct comparison of the predation rates in the two seed species was possible because the respective experiments were done at different time periods. Therefore, all analyses were done separately for the two species. We also present separate models for structurally rich and structurally poor forest edges, because initial exploratory analyses revealed that differences between the two edge types confounded all other effects. The statistical analyses followed Zar (1996); the calculations were done with the programme JMP® (SAS Institute. 1995).

Results

Seed predation at the edge sites

In the structurally rich sites, seed predation decreased significantly with distance to the forest edge for both *Prunus avium* and *Viburnum lantana*, whereas no such effect occurred in the structurally poor sites (Table 1). In the rich sites predation decreased strongly within the first 25 m, whereas little differences were found between the plots at 25 m and at 50 m (Figure 1). Near the edge (1–6 m) 90–100% seed predation was observed contrasting with 60–70% towards the forest interior. In some sites the predation rate even increased between 25 m and 50 m. This result might be due to small canopy gaps which caused a local increase in ground vegetation. No clear trend emerged in the structurally poor sites, although seed losses were slightly reduced for the plot at 1 m from the edge line, and predation of *Prunus avium* increased for the 50-m plots. In no site a significant *edge site* × *distance* interaction occurred ($P > 0.05$), although in the structurally poor sites the logistic model was better which included the interaction term (Table 1). This result is probably explained by higher variation among the sites with structurally poor forest edges.

The temporal course of seed removal from the dishes followed a negative exponential relationship (M. Buschor, unpubl. data). Mostly in the structurally rich sites all seeds were gone after the first day, whereas in some of the poor sites even after four days no seeds were removed. We observed strongest losses within the first week; afterwards removal rates dropped considerably. After 16 days at all structurally rich sites at least 72% of the *Prunus avium* dishes were empty, and 66% in *Viburnum lantana*. At the structurally poor sites 61% of the *Prunus* dishes were gone and 11% of those with *Viburnum* seed. Variation in the temporal course of seed predation was stronger in the structurally poor sites and slightly higher in *Prunus*. No effect of forest age, community type, slope or aspect was observed.

Seed predation and vegetation structure

Seed predation increased with cover of the herb and shrub layer (Figure 2), and for both species and both edge types the herb+shrub cover had highest predictive power explaining variation in predation. Neither litter, tree density nor density of dead wood showed a significant correlation with the predation rates. The only exception was *Viburnum lantana* in structurally rich sites where a significant negative correlation was observed with dead wood (Wald $\chi^2 = 4.55$, $P = 0.03$).

Both in structurally rich and in structurally poor edges there was a significant decrease in herb and shrub cover from the forest edge towards the interior (Figure 3, Table 2). The only exception was a site where the most distant plot had a shrub cover of about 85%, whereas in the other 50-m plots cover was 30–50%. This exception was caused by locally dense recruitment of *Fagus sylvatica*, most likely caused by a

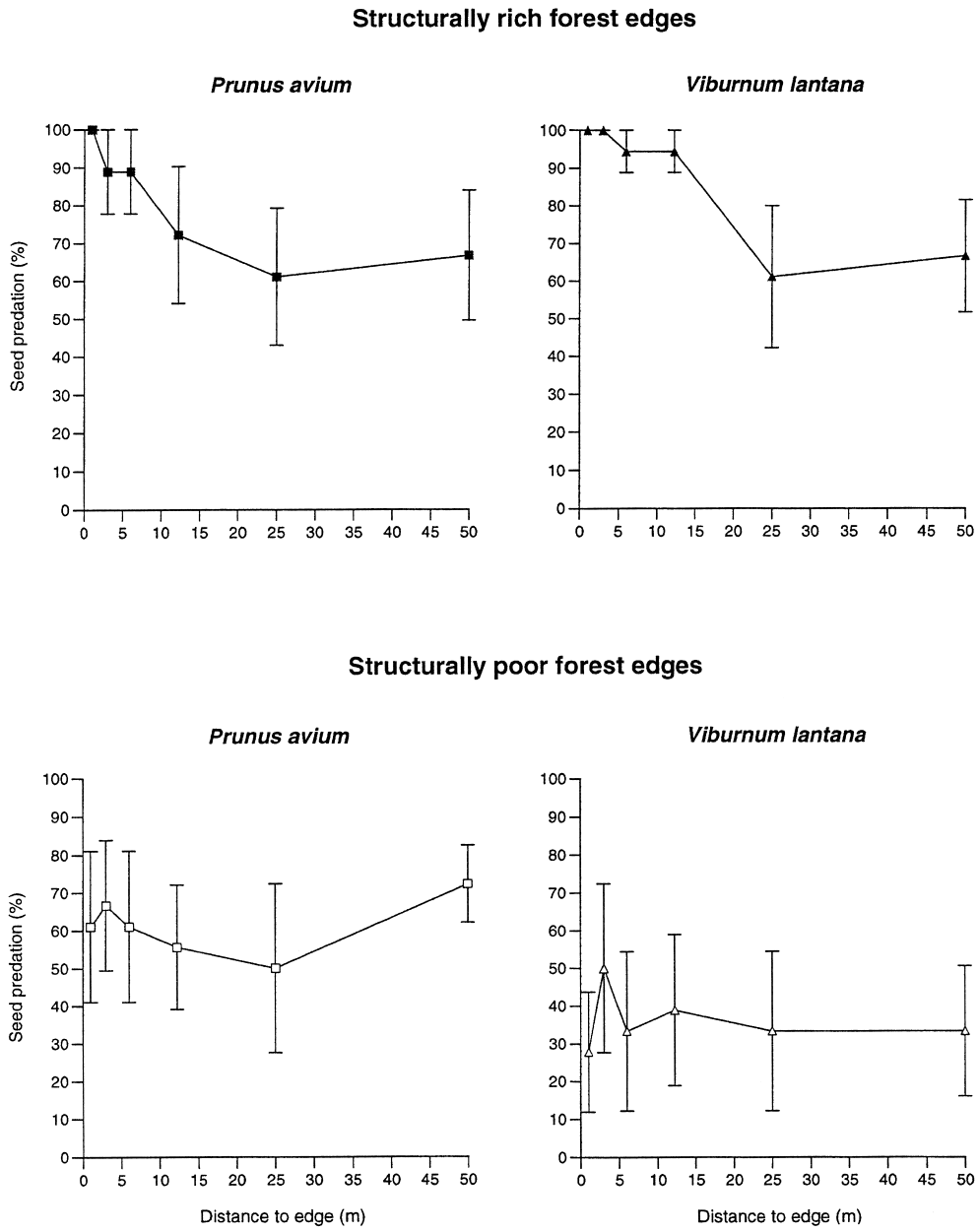

Figure 1. Spatial pattern in seed predation of *Prunus avium* and *Viburnum lantana* at structurally rich and structurally poor forest edges. Predation rate is given as mean percentage of empty seed dishes (±SE) in six plots with 1–50 m distance to the edge (n = 18 dishes per distance plot, i.e. three transects in six sites, respectively). For statistical results see Table 1.

former gap in the tree canopy. Thus, this plot was excluded from further analyses.

Seed-predating animals

Rodents were most likely responsible for seed removal in the present structured comparison. With few exceptions no seeds were removed from those dishes which were accessible only to molluscs or insects (2.3% of 216 dishes in *Prunus*, 1.4% in *Viburnum*), whereas most seeds disappeared from the dishes accessible to small mammals or birds. In all study sites the presence of urine, droppings and seed remnants indicated that rodents were the major granivores.

The live-trapping confirmed the presence of the rodent species *Apodemus flavicollis* Melch., *Apode-*

Table 1. Edge effects in seed predation of *Prunus avium* and *Viburnum lantana* at (a) structurally rich forest edges, and (b) structurally poor edges. Edge effects are indicated by significant results of the logistic regression models for the variable "distance" to the forest edge (1–50 m). No significant interaction between distance and edge site was observed.

Seed species	G^2 (P value)	Wald χ^2 (P)	Regression coefficient (±SE)	AICc
(a) Structurally rich forest edges (n = 108, df = 6)				
Prunus avium	57.1 (< 0.0001)	Distance, 9.35 (0.0022)	–0.072 ± 0.023	67.2
		Edge site, 8.50 (0.13)		
Viburnum lantana	38.8 (< 0.0001)	Distance, 12.8 (0.0004)	–0.0088 ± 0.025	59.3
		Edge site, 7.58 (0.18)		
(b) Structurally poor forest edges (n = 108, df = 6)				
Prunus avium	72.2 (< 0.0001)	Distance, 5.2 10^{-5} (0.99)	–0.010 ± 1.455	99.4
		Edge site, 16.5 (0.006)		
		Distance × site, 11.0 (0.05)		
Viburnum lantana	110.9 (< 0.0001)	Distance, 0.004 (0.95)	–0.875 ± 13.9	57.6
		Edge site, 4.20 (0.52)		
		Distance × site, 1.78 (0.88)		

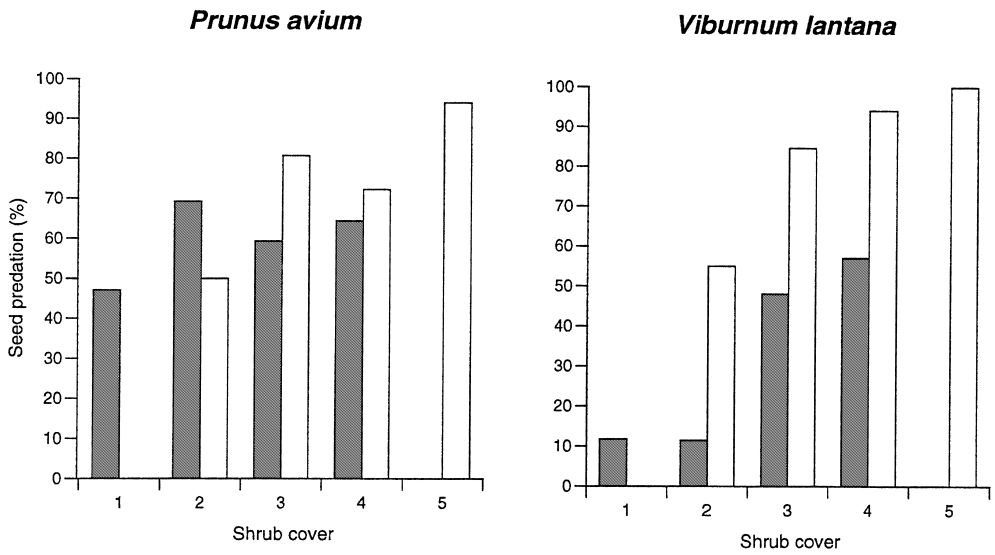

Figure 2. Seed predation of the two study species in relation to shrub (and herb) cover at the study plots. Vegetation cover at 0–3 m height (3 × 3 m^2 plots) was estimated in five classes: 1, 0–20%; 2, 21–40%; 3, 41–60%; 4, 61–80%; and 5, 81–100%. Seed predation was positively correlated with vegetation cover in *Prunus avium* (structurally rich edges, Wald χ^2 = 3.73, P = 0.05; structurally poor edges, χ^2 = 7.71, P = 0.006), as well as in *Viburnum lantana* (χ^2 = 7.89, P = 0.005; χ^2 = 4.97, P = 0.026). Structurally rich edges have open bars; structurally poor edges filled bars.

mus sylvaticus L. and *Clethrionomys glareolus* Schreber. In mid June the apparent rodent density was slightly lower than in early August (0.15 *vs* 0.19 rodents trap^{-1} night^{-1}). *Apodemus* spp. was always more frequently trapped than *Clethrionomys glareolus*. In June 89% of the rodents (n = 97) were *Apodemus* spp., in August 75% (n = 127). In June 68% and in August 64% of the rodents were trapped in structurally rich forest edges (Figure 4). The difference between the habitat types was significant in both time periods (June: χ^2 = 8.6, df = 1, P = 0.0034; August: χ^2 = 11.3, df = 1, P = 0.0008), although the relative abundance of *Apodemus* spp. was similar in structurally rich and poor forest edges (June: 89% *vs* 87%, respectively; August: 83% *vs* 62%).

More rodents were trapped in sites which showed high intensity of seed predation (*Prunus vs* first trapping period: χ^2 = 15.2, df = 1, P < 0.0001; *Viburnum vs* second trapping period: χ^2 = 28.9, df = 1, P < 0.0001). Herb and shrub cover was the only variable of the vegetation structure which correlated (positively) with the abundance of rodents both in structurally

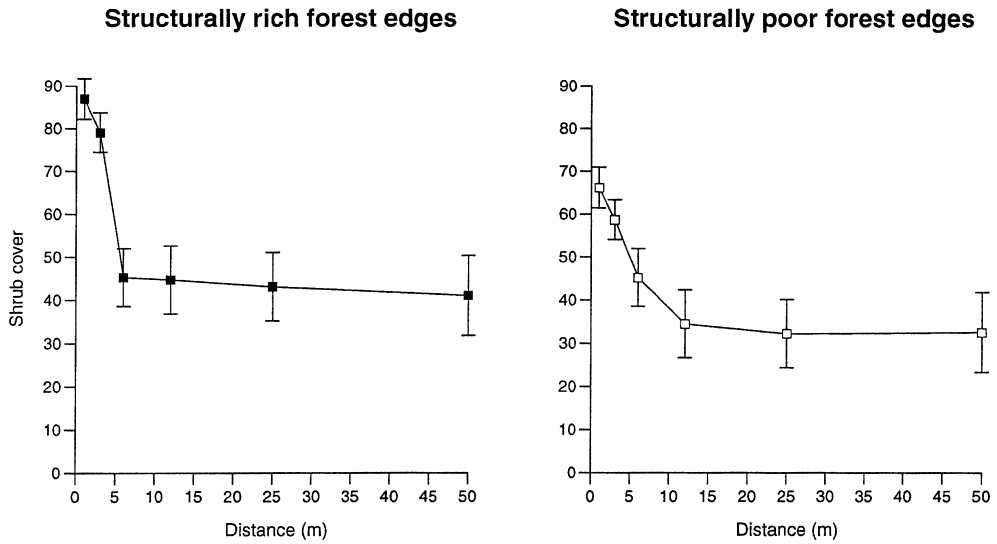

Figure 3. Shrub (and herb) cover as a function of distance to the forest edge in structurally rich and structurally poor sites (0–50 m; means ± SE).

Table 2. Herb and shrub cover at 0–3 m height in relation to the distance from the forest edge (n = 108, df = 11).

Forest edge type	F value (P)	F value of factors (P)	Regression coefficient (±SE)	r^2_a
Structurally rich	3.54 (0.0003)	Distance, 23.4 (< 0.0001)	–0.008 ± 0.0017	0.21
		Edge site, 1.11 (0.36)		
		Distance × site, 1.93 (0.096)		
Structurally poor	5.51 (< 0.0001)	Distance, 21.2 (< 0.0001)	–0.005 ± 0.0013	0.34
		Edge site, 1.76 (0.13)		
		Distance × site, 3.95 (0.0027)		

rich and in structurally poor forest edges and in both time periods (logistic regression: Wald $\chi^2 > 4.1$, $P < 0.05$). No significant effect was observed for litter cover, density of trees and dead wood.

Discussion

Edge effects in seed predation

A clear edge effect, i.e. decreasing seed predation with increasing distance to the forest edge was observed for structurally rich forest edges. A similar result of higher seed predation in edge habitats compared with forest interior was reported by Jules and Rathcke (1999) for *Trillium ovatum* (Liliaceae) in montane conifer forest in Oregon. Sork (1983), on the other hand, found that fewer nuts of *Carya glabra* were consumed near the edge of a temperate forest. However, in this study the seeds were buried in the soil and could have attracted a different set of predators which are less dependent on vegetation cover for predator avoidance which is a key behaviour in small mammals (Bowers and Dooley 1993; Hulme 1998). The remaining studies on seed predation near forest edges were done in tropical rainforest, and they produced conflicting evidence for edge effects as described in the Introduction (Burkey 1993; Osunkoya 1994; Notman et al. 1996; Holl and Lulow 1997; Tabarelli and Mantovani 1997; Wong et al. 1998; Restrepo and Vargas 1999). Differences in climate, structure of the forest edge, and in the species pool of seed predators may be responsible for these results. Clearly, the findings of our study suggest that a more precise description of the structural edge characteristics would facilitate the aspired comparison among published studies. Some of the contrasting results may actually be caused by changes in the vegetation near the edge and are not simply a result of the forest edge *per se*. Thus, we agree with Paton (1994); Murcia (1995); McCollin (1998) that despite the considerable number of studies on edge effects conclusions

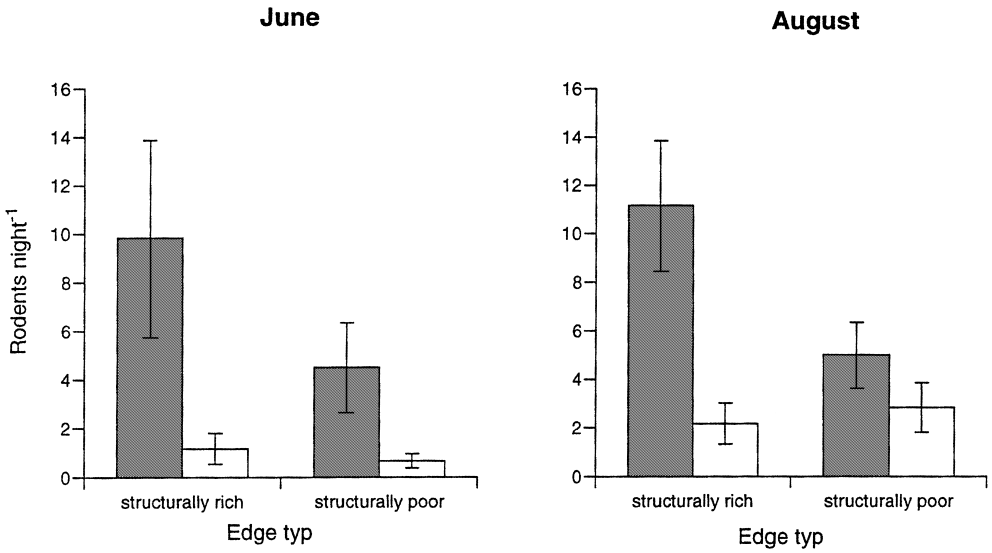

Figure 4. Rodent abundance at the two types of forest edge (means ± SE). Rodents were caught in Sherman live-traps for three nights in June and August (n = 108 traps). In June 97 rodents were caught, in August 127 rodents (filled columns, *Apodemus flavicollis* and *A. sylvaticus*; open columns, *Clethrionomys glareolus*). In both time periods significantly more rodents were caught at structurally rich forest edges (Chi-square test of independence: June, χ^2 = 8.6, P = 0.0034; August, χ^2 = 11.8; P = 0.0008).

are difficult due to poor research design and lack of consistency in methods.

One potential problem of our study is the spatial range over which a possible edge effect was investigated. Although the review of Murcia (1995) indicates that most abiotic and biotic edge effects are found within 20–50 m from the edge line, some authors argue that true forest interior conditions need at least 100–500 m distance to any forest edge (reviewed by Paton (1994)). For example the study of Jules and Rathcke (1999) investigated spatial patterns in seed predation up to 332 m from the edge line. In our study it was not possible to investigate forest plots > 50 m from treefall gaps, clear cuts or forest roads, although the forest stands continued at least 0.5 km from the edge sites. Moreover, investigating longer transects would have added to the heterogeneity of the sample, because of changes in topography, soil type and community structure. A transect of 50 m length is relatively short compared with rodent home ranges which can have up to 300 m diameter (e.g. Szacki (1999)). However, the significance of a local edge effect is not violated by movements of rodents along transects or even between transects. Concerning the population dynamics of the study plants an "edge effect in seed predation" depends solely on local abundance and activity of the rodents which is strongly affected by vegetation structure.

Vegetation structure and seed predation

The observed edge effect was most likely caused by locally increased herb and shrub cover and not by the forest edge *per se*. However, high density of shrubs and herbs is a common feature of most forest edges (Ranney et al. 1981; Richert 1996). Herb and shrub cover had a significant effect on the predation rates in both study species and cover values were affected by the distance to the edge line. Thus, we conclude that the cover of the shrub layer was the main reason for the edge effect in structurally rich sites. This leads to the question why no such effect was observed in the structurally poor sites, although they also showed decreasing shrub cover with increasing distance from the edge. One reason might be that shrub cover in the structurally rich sites was higher near the edge than in the poor sites. A dense shrub belt reduces light conditions inside the forest leading to a steeper gradient in ground vegetation cover towards the forest interior (cf. Figure 3). Clearly, the correlation between distance and vegetation cover was weaker in the structurally poor forest edges.

A positive correlation between seed predation and shrub cover is a key finding of the present study, because it was found for both time periods and independent of the structural diversity of the edge site. Certainly, one might argue that this correlation indicates not necessarily a direct causal relationship, and fur-

ther studies are necessary to investigate this question. However, there is ample evidence in the literature (summarized by Hulme (1998)) that vegetation cover has a significant influence on seed predation because of higher rodent abundance (Hay and Fuller 1981; Mittelbach and Gross 1984; Webb and Willson 1985; Gill and Marks 1991; Kollmann 1995; Hau 1997; Hulme 1997). Explanations for the preference of rodents for patches of dense vegetation include avoidance of predators, higher food abundance and microclimatic traits (Thompson 1982; Simonetti 1989). Clearly, some of these factors are tightly correlated (McCollin 1998). For the rodent species of the present study (*Apodemus flavicollis, A. sylvaticus, Clethrionomys glareolus*) several publications have demonstrated preference of dense woody vegetation and avoidance of open habitats (e.g. Schlund and Scharfe (1995); Kozakiewicz et al. (1999)).

The observed negative correlation between predation and density of dead wood was probably a spurious result, because density of dead wood correlated also negatively with shrub cover. However, Whelan et al. (1990) also reported lower seed predation near dead logs and at the base of trees compared with open forest floor for *Cornus drummondii* but not for *Prunus serotina*. The lack of a correlation between rodent abundance and density of trees, dead wood or litter cover might be a result of pooling the rodent species, because they have different habitat preferences (Schlund and Scharfe 1995; Kozakiewicz et al. 1999). We made no separate analyses for the three rodent species, because it was not possible to separate the species-specific contribution to seed removal from the experimental dishes.

Identity of the seed predators

Because there was virtually no removal of seed from the control dishes, we conclude that rodents were the main predators of the two study species, whereas insects and molluscs were of minor importance as also observed for large forest seed in other temperate forest ecosystems (e.g. Schwantes Boman and Casper (1995); Kollmann et al. (1998); Hulme and Borelli (1999); reviewed by Hulme (1998)). Seed predation by birds is unlikely, because only the hawfinch (*Coccothraustes coccothraustes*) is able to open *Prunus* seed (Snow and Snow 1988), and this bird is very rare in the study area. Seeds of *Viburnum lantana* are less well protected and might be accessible, for example to chaffinch (*Fringilla coelebs*) or blue tit (*Parus caeruleus*). Clearly, the contribution of passerine birds to edge effects in seed predation needs to be checked in future studies, although from previous experience in similar habitats the influence of birds seems to be rather low (Kollmann and Muir 1998; Kollmann et al. 1998; Kollmann and Bassin 2001).

Neither the absolute nor the relative abundance of rodent species can be derived from our data, because the rodents were not labelled. Moreover, estimates on abundance of *Clethrionomys glareolus* might be too low because we only trapped during the night, and *Clethrionomys* has higher activity during the day compared with the two *Apodemus* species (Niethammer and Krapp 1978, 1982). To get a more adequate picture of the rodent abundance, more frequent trapping and labelling of the animals might be desirable (Kozakiewicz et al. 1999; Szacki 1999). This would also detect movements of rodents along or between transects.

Seed predation and plant population dynamics

Seed predation is expected to affect population dynamics of *Prunus avium* and *Viburnum lantana*, because these woody species have little vegetative reproduction, no masting, no seed bank and the seeds are highly attractive (Kollmann 1996; Kollmann et al. 1998). However, although seed predation is a key process during regeneration of plant populations, caution is needed when predicting demographic trends of long-lived woody species from short-term experiments (Crawley 1992; Hulme 1996). Moreover, not all cases of seed removal will lead to mortality, because rodents cache seeds and the associated secondary dispersal might actually enhance regeneration (Jensen and Nielsen 1986; Vander Wall 1990).

In the study species, microsite limitation in regeneration will vary with the spatio-temporal patterns in seed rain and seedling establishment (Kollmann 1995). Along forest edges in the temperate zone the density of fleshy-fruited plants is particularly high (Kollmann 1997; Kollmann and Schneider 1999), and bird-mediated seed rain is most likely increased compared with the forest interior (Hoppes (1988); M. Pirl & J. Kollmann, unpubl. data). One reason might be that abundance of frugivorous birds is often higher near forest edges and in gaps (Hoppes 1987; Levey 1988; McCollin 1998; Restrepo et al. 1999). Intensive seed predation near the edge might counterbalance increased seed rain, as observed for various stages of shrub development in abandoned grassland (Koll-

mann 1995). However, unfavourable light conditions in dense scrub can be an even more important bottleneck for regeneration of fleshy-fruited species (Kollmann and Reiner 1996; Kollmann and Grubb 1999). Therefore, the consequences of higher seed predation near temperate forest edges remain to be investigated, as done by Jules and Rathcke (1999) for population dynamics of *Trillium ovatum*.

Seed predation was most intense in the first week. This result is similar to the observations of Whelan et al. (1990); Kollmann et al. (1998). The main reasons might be decreasing density of seed and decreasing odour, because rodents locate seed by odour (Price and Jenkins 1986). Undoubtedly, the first weeks are crucial for seed survival. Survival is markedly increased if during this period seeds are covered by soil and litter (Barnett 1977; Myster and Pickett 1993; Hulme and Borelli 1999). It would be interesting to know whether or not litter fall and soil dynamics are increased near the forest edge, as observed for recently created forest edges in central Amazonia by Sizer et al. (2000).

There was a slight tendency towards higher seed predation in *Prunus avium*, although rodent abundance was higher in late July when the predation experiment with *Viburnum lantana* was done. This result is in accordance with earlier observations of higher attractivity of *Prunus avium* seed compared with *Viburnum lantana* (Kollmann et al. 1998). Long-term differences in seed survival might explain some of the variation in abundance of the two species along forest edges (Kollmann and Schneider 1999).

Conclusions

The central objective of the study was to investigate the significance of edge effects *per se* compared with indirect effects mediated by changes in vegetation structure close to the edge. The results of the study demonstrate that edge effects *per se* are of little importance. Instead, there are abiotic and biotic factors that change at forest edges, and these can have complex indirect effects on forest processes. For forests with a dense shrub and/or herb cover close to the edge and rather sparse ground vegetation in the forest interior we expect a clear edge effect in seed predation, and this forest type is rather common in central Europe. If the ground vegetation is missing at the edge or if the interior has also a dense ground cover due to a more open canopy, then we predict no edge effect to occur. Thus, edge effects in the same region and for the same forest community may change with management or successional state of the forest stand. General "edge rules" without clear description of the vegetation structure are not promising, especially when including edges of different forest types, at different altitudes or in different biomes. Further research on edge effects in seed predation should focus on the mechanisms of the edge effects and on the consequences of the observed patterns in seed predation for plant population dynamics.

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